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Lack of an association between plasma follicle-stimulating hormone concentrations and ovarian weight in prepubertal gilts[1]

J. J. Ford[2], T. H. Wise, and R. K. Christenson

ARS, USDA, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933-0166

ABSTRACT: Selection for increased number of corpora lutea in gilts is associated with increased plasma FSH concentrations during pubertal development. In the current study, 270 gilts from a control (CO) line and a line selected for increased ovulation rate (OR) were unilaterally ovariectomized at 85 d of age, and this ovarian weight was related to FSH concentrations at 65, 75, and 85 d of age. Gilts were produced during two farrowing seasons, spring and fall, and the age at first estrus was monitored from 160 to 250 d. Plasma FSH was greater in OR than in CO gilts at 65 ($P < 0.01$) and 75 d (difference in spring greater than in fall, $P < 0.01$), but FSH at these ages was not correlated with ovarian weight at 85 d. At 85 d, FSH did not differ in gilts of these lines; however, FSH was negatively correlated ($r = -0.27$, $P < 0.01$) with ovarian weight. The proportion of gilts detected in estrus was less for spring-born CO gilts than for spring-born OR or for fall-born CO and OR gilts (78 vs. 92%, season × line, $P < 0.02$). The age at first estrus was similar in the two lines but was earlier ($P < 0.01$) for spring-born than for fall-born gilts (194 vs. 204 d). Concentrations of FSH at each of the ages examined were not correlated with the age at first estrus. These observations support the conclusion that selection for a greater number of corpora lutea produces a correlated increase in plasma FSH during early pubertal development. This increase in FSH most likely reflects differences in FSH synthesis and release and not differences in the stage of pubertal development.

Introduction

Ovarian follicles bind follicle-stimulating hormone (FSH) beginning at the primary stage of development (Findlay and Drummond, 1999), with a functional response in porcine follicles at the secondary stage (Morbeck et al., 1993). Ovulation is difficult to induce with exogenous gonadotropins in early prepubertal gilts (Casida, 1935; Oxender et al., 1979), improves with increasing BW (Britt et al., 1989), and varies with genotype (Tilton et al., 1995). Likewise, the ovulatory response to exogenous gonadotropin-releasing hormone increases with advancing age after 70 d (Pressing et al., 1992). We established that selection for greater number of corpora lutea produced greater plasma concentrations of FSH during prepubertal development in three different populations of gilts relative to their respective control lines (Cassady et al., 2000; Ford et al., 2001). As a consequence of these findings, we questioned whether ovarian development during prepubertal development differed in gilts of the selected line relative to the control line from which they were derived. Moreover, in these populations of gilts, the impact of selection for greater number of corpora lutea on the rate of pubertal development had not been evaluated. Potential differences in the rate of sexual development could contribute to differences in FSH secretion. The current study evaluated ovarian weight at 85 d of age, age at first estrus, and the proportion of gilts detected in estrus by 250 d of age in addition to reevaluation of plasma FSH concentrations during prepubertal development in two lines divergent in ovulation rate.

Materials and Methods

Gilts

Gilts were a four-breed composite established from purebred pigs obtained from 1973 to 1977 (Young et al., 1986). A four-breed composite of Chester White,

Landrace, Large White, and Yorkshire was formed in 1981 (Cassady et al., 2002a). Beginning in 1988, one line was selected for 10 generations for a single trait, increased number of corpora lutea (**OR**), whereas a control line (**CO**) was maintained as randomly selected (Christenson et al., 1987; Leymaster and Christenson, 2000). In the current study, first-litter sows produced gilts in the third year of relaxed selection (OR, n = 137 from 26 sires; CO, n = 139 from 24 sires). Gilts were from two 3-wk farrowing seasons; 140 were born in September, and 136 were born in March. Each boar sired gilts in only one season. Gilts were weaned at a mean age of 18.2 d (range of 15 to 21 d) and moved to a nursery, after which they were placed in a finishing building at a mean age of 66 d, seven to nine gilts per pen. During rearing in the nursery and finishing building, gilts had free access to water and corn-soybean meal diets. Percentage CP and ME in diets, respectively, were 21.5% and 3.43 Mcal/kg from 2 to 5 wk of age, 20.9% and 3.51 Mcal/kg from 5 to 8 wk of age, 18% and 3.35 Mcal/kg from 8 to 12 wk of age, 16% and 3.38 Mcal/kg from 12 to 16 wk of age, and 15% and 3.39 Mcal/kg from 16 to 22 wk of age. Blood samples were collected by jugular venipuncture at mean ages of 65 and 75 d, range = 4 d. Gilts were in the finishing building at least 7 d before a subsequent blood sample was taken. At a mean age of 85 d, gilts were moved by pen to a preoperative surgery building. Diet and water were withheld overnight followed by blood sampling of each gilt the next morning. Anesthesia was induced and maintained under halothane; one ovary was removed after high lumbar laparotomy; side of ovariectomy was alternated within littermate gilts. Following recovery from anesthesia, gilts were returned to their original pen in the finishing building. As the oldest gilt in a pen approached 160 d of age, gilts from multiple pens were weighed, moved to a gilt development building, and reallocated based on BW to pens of 10 or 11, with ≥1.3 m^2/gilt. At this time, gilts were fed once daily as a group (1.81 kg/gilt, 12.5% CP, and 3.28 Mcal/kg). With the exception of subtle changes in diet formulation and greater number of dietary changes during the growing and finishing phases, this is the management protocol used since the parental line of these gilts was formed in 1981 (Cassady et al., 2002a). Also at this time, once-daily detection of estrus was initiated. Three to four mature boars (>11 mo of age) were placed in a pen between two pens of gilts, during which time herdsmen applied back pressure to gilts within each pen. Of the 276 gilts assigned to this study, 270 were evaluated for age at puberty, 5 were removed for health reasons, and 1 was found to have an ovotestis. Gilts were slaughtered during the luteal phase after each had expressed two estrous periods 17 to 25 d apart; ovaries were collected and dissected, and the number of corpora lutea were counted. Gilts that failed to have regular estrous periods by 250 d of age were slaughtered, and the reproductive tract was examined for normality and stage of development. The number of corpora lutea was not ob-

tained on 11 of the 238 gilts that showed pubertal estrus, due to conflicts with the scheduling of slaughter. Body weights were recorded at birth, weaning, mean ages of 56 and 154 d, and day of slaughter. Procedures for handling gilts complied with those specified in the *Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching* (FASS, 1999).

FSH RIA

Plasma samples were stored at –20°C until FSH concentrations were estimated by standard RIA procedures (Trout et al., 1992), but porcine FSH (AFP10640B) was used for both iodination and as the reference preparation in combination with anti-porcine FSH (AFP2062096Rb). Interassay CV were 16.8% for a pool of serum that assayed 1.9 ng of FSH/mL, and 10.3% for a pool from ovariectomized gilts that assayed 3.8 ng of FSH/mL. Plasma FSH concentrations on each day of collection were evaluated in separate assays.

Statistical Analysis

Concentrations of FSH, ovarian weight, BW, ages at first estrus, and the number of corpora lutea were evaluated statistically using Harvey's mixed model procedure (Harvey, 1977). The model included fixed effects of the four combinations resulting from two genetic lines, and two seasons plus the random effects of sire within line, and litter within line × sire. Interactions of genetic line with season were not significant (*P* > 0.10) if not stated. Correlation analyses, within Harvey's mixed model procedure, account for contributions of the main effects within the model. Data are presented as least squares means.

Results

Body weight at birth and weaning did not differ among lines (Table 1), but, by 56 d of age, CO gilts weighed more (*P* < 0.01) than OR gilts, and this difference persisted through 154 d of age. Season of birth had no influence on birth weight, but, at weaning and later ages, fall-born gilts weighed more (*P* < 0.01) than spring-born gilts. The weight of a single ovary at 85 d ranged from 0.05 to 2.34 g and was not influenced by genetic line or season (Table 1). At least one antral follicle was detected on 46 and 41% of the ovaries from CO and OR gilts, respectively. Ovarian weight at 85 d was not correlated (r = 0.06) with BW at 56 d of age.

At 65 d of age, plasma FSH concentrations were 19% greater (*P* < 0.01) in OR gilts and were not affected by season (*P* > 0.10; Figure 1A). At 75 d, FSH remained higher in the OR gilts (Figure 1B); this was due to a greater difference in the spring but not in the fall (line × season; *P* < 0.01). At 85 d, FSH concentrations were similar in both lines and were somewhat greater in the spring than in the fall (*P* < 0.06; Figure 1C). Plasma FSH concentration in all gilts at 65 d were correlated

Table 1. The influence of genetic line and season on body and ovarian weights of prepubertal gilts

Item	No. of gilts	Birth wt, kg	Weaning wt, kg	56-d wt, kg	154-d wt, kg	d-85 ovarian wt, g
Line[a]						
CO	135	1.34 ± 0.02	4.81 ± 0.09	17.5 ± 0.19**	81.8 ± 0.86*	0.47 ± 0.06
OR	135	1.29 ± 0.02	4.75 ± 0.09	16.2 ± 0.19	79.0 ± 0.87	0.47 ± 0.06
Season						
Spring-born	133	1.33 ± 0.02	4.61 ± 0.09	15.5 ± 0.20	77.7 ± 0.86	0.41 ± 0.07
Fall-born	137	1.30 ± 0.02	4.94 ± 0.09**	18.2 ± 0.18**	83.0 ± 0.86**	0.53 ± 0.06

[a]CO = control line and OR = line selected for ovulation rate.
*$P < 0.05$ and **$P < 0.01$ for comparison between lines or seasons.

($P < 0.01$) with those at 75 d (r = 0.52) and those at 85 d (r = 0.33), as were concentrations of FSH at 75 d correlated with those at 85 d (r = 0.32; $P < 0.01$). Ovarian weight at 85 d of age was not correlated with plasma FSH at 65 or 75 d of age (r = 0.17 and –0.08, respectively), but ovarian weight and plasma FSH concentration at 85 d were correlated negatively for the two lines combined (r = –0.27; $P < 0.01$).

The proportion of gilts detected in estrus by 250 d of age was 9.2% greater in OR than CO gilts (Figure 2A) due to a 17.4% difference between lines in the spring; the difference in the fall was not significant (line × season; $P < 0.02$). The age at first detected estrus for those that expressed estrus was similar ($P > 0.30$) for CO and OR gilts (range = 170 to 246 d; Figure 2B). However, first estrus occurred at a younger age ($P < 0.01$) in spring- vs. fall-born gilts. Body weight at 154 d in gilts that expressed estrus by 250 d was similar to that of gilts classified as acyclic (80.2 ± 0.7 vs. 81.8 ± 1.6 kg). The age at first estrus was not correlated with BW at 56 d (r = –0.06) or at 154 d (r = –0.14) of age or with ovarian weight at 85 d (r = –0.04). Mean daily weight gain from 154 d of age until puberty was not influenced by line or season (0.47 ± 0.009 kg/d; $P > 0.10$).

The number of corpora lutea was greater ($P < 0.01$) in OR than in CO gilts and was greater ($P < 0.01$) in fall-born than in spring-born gilts (Table 2; range = 9 to 26 corpora lutea). In all gilts, the number of corpora lutea increased with increasing weaning weight (r = 0.20; $P < 0.05$), 56-d weight (r = 0.28; $P < 0.01$), 154-d weight (r = 0.27; $P < 0.01$) and slaughter weight (r = 0.28; $P < 0.01$), but the number of corpora lutea was not correlated with birth weight (r = 0.11), d-85 ovarian weight (r = –0.10), or age at first estrus (r = 0.11).

Discussion

The present study reaffirmed that ovulation rate was greater in OR gilts, that selection for a greater number of corpora lutea produced an associated increase in concentrations of plasma FSH in prepubertal gilts and that the difference in FSH concentrations between the two lines disappeared by 85 d of age (Ford et al., 2001). The observation of increased plasma FSH concentrations in prepubertal gilts of two other genetic lines that were selected for a greater number of corpora lutea (Cassady et al., 2000; Ford et al., 2001) supports the observation that greater FSH secretion is a response correlated with selection rather than with random genetic drift. The negative feedback loop for the regulation of FSH is inoperative during early prepubertal development in gilts due to inadequate ovarian secretions (Colenbrander et al., 1987); thus, differences between OR and CO gilts in plasma FSH at 65 and 75 d of age most likely reflect differences in the synthesis and secretion of FSH. Plasma FSH concentrations decreased with age after 75 d, as observed in earlier studies (Diekman et al., 1983; Camous et al., 1985; Cassady et al., 2000), and, by 85 d, they were negatively correlated with ovarian weight. These changes in FSH concentrations are indicative of the maturation of negative feedback regulation (Colenbrander et al., 1987; Prunier and Louveau, 1997) and reflect the development of antral follicles (Oxender et al., 1979; Dyck and Swierstra, 1983), with their greater capacity for inhibin and estrogen secretion. Sampling at more frequent intervals in the current study than in our earlier study provided support that maturation of negative feedback regulation occurs at a similar age in both CO and OR gilts.

In Meishan crossbred pigs, QTL for ovulation rate map to chromosomes 8 and 10, and QTL for plasma FSH concentrations in boars map to these same genomic regions (Rohrer et al., 1999; Rohrer et al., 2001; Nonneman and Rohrer, 2003). The importance of these findings to the current lines of pigs remains to be established. To date, genomic scans or linkage analyses have not been conducted in the CO and OR lines.

Ovarian development, assessed by weight at 85 d of age, the primary objective of the study, was similar in CO and OR gilts. Consequently, ovaries of OR gilts were not responding to the greater concentrations of FSH in their circulation from 65 to 75 d of age in a manner that produced changes in ovarian weight. Differential changes in the composition of ovaries cannot be ruled out. An explanation for this lack of responsiveness is not apparent as Morbeck et al. (1993) determined that the proliferation in vitro of granulosa cells from second-
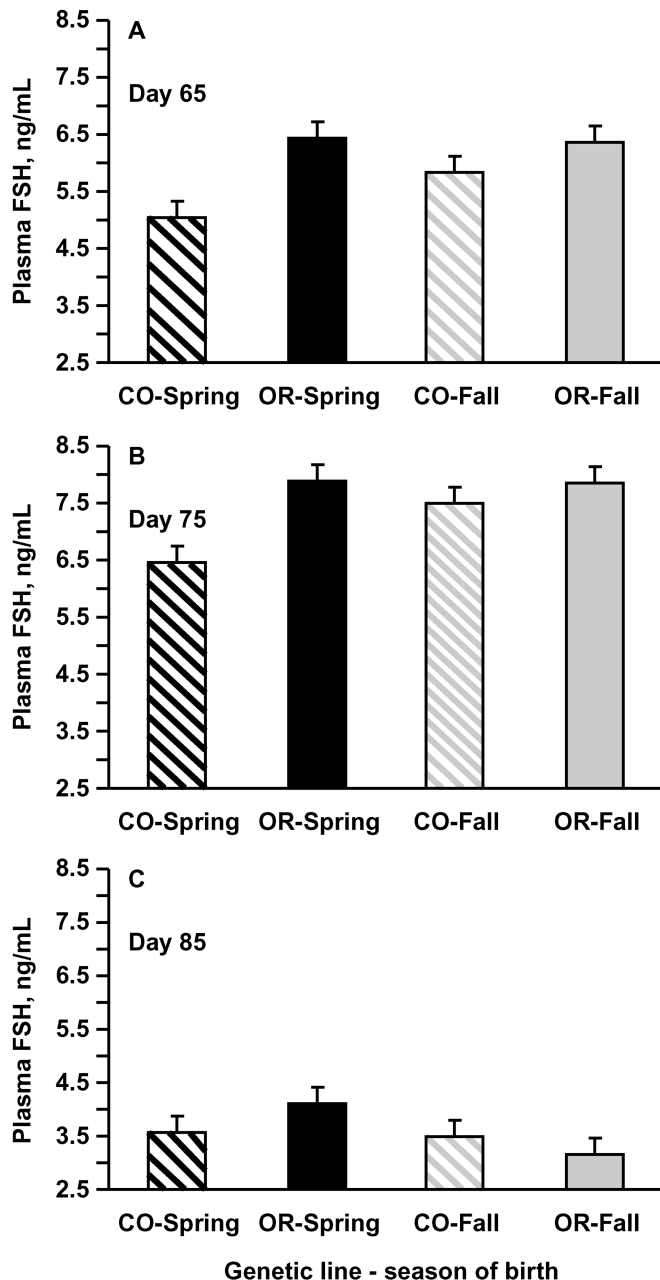
Figure 1. Plasma FSH concentrations in prepubertal gilts of the Control (CO, n = 135) and Ovulation Rate (OR, n = 135) lines. Gilts were born either in the spring (n = 133) or in the fall (n = 137). A) Plasma samples collected at 65 d of age; OR > CO, $P < 0.01$. B) Plasma samples collected at 75 d of age; line × season, $P < 0.01$. C) Plasma samples collected at 85 d of age; spring > fall, $P < 0.06$.

Figure 2. Pubertal development in gilts of the Control (CO) and Ovulation Rate (OR) lines. Gilts were born either in the spring or in the fall. A) The percentage of gilts that were detected in estrus by 250 d of age; line × season, $P < 0.02$; n = 65 to 69 for each line × season subgroup. B) The mean age at first estrus for gilts detected in estrus by 250 d of age; fall > spring, $P < 0.01$; n = 114 CO gilts and 124 OR gilts, of which 115 were born in the spring and 123 in the fall.

d of culture in media that contained serum. In contrast to the above observations, preantral follicles obtained from gilts at 84 to 105 d of age and cultured in serum-free medium grew at a slower rate, and fewer of these follicles formed an antrum (Shuttleworth et al., 2002). The slower growth most likely reflects the use of serum-free medium, but the impact of obtaining follicles from younger gilts has not been evaluated.

Exogenous gonadotropins fail to stimulate discernible follicular growth and ovulation in gilts younger than 50 d of age (Casida, 1935; Kather and Smidt, 1975; Oxender et al., 1979), but, after 60 d, the proportion of gilts that ovulate in response to exogenous gonadotropins increases with age as does the proportion of gilts that possess antral follicles. Morbeck et al. (1993) proposed that gilts without antral follicles would not show a noticeable response to 5 d of exogenous gonadotropins due to the slow growth rate of preantral porcine follicles (Morbeck et al., 1992). Previously, we observed that the OR gilts had greater circulating concentrations of FSH

ary follicles of 50- to 60-d-old gilts increased after treatment with FSH, but FSH did not affect the proliferation of granulosa cells from primary follicles of neonatal gilts. Furthermore, FSH stimulated the growth in vitro of porcine preantral follicles obtained from gilts greater than 150 d of age (Wu et al., 2001; Mao et al., 2002); an antrum formed in many of these follicles within 4
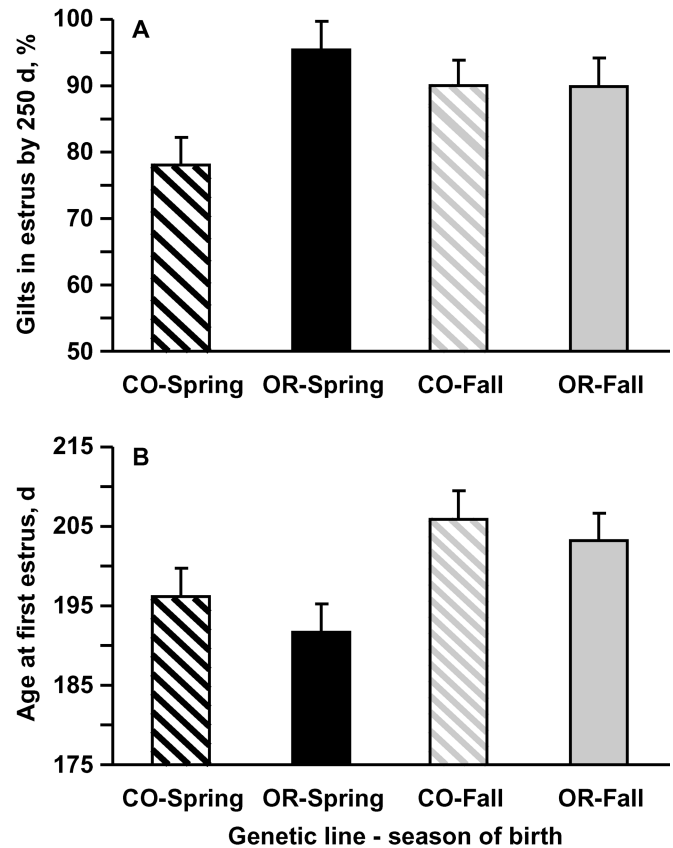
Table 2. The influence of genetic line and season on the number of corpora lutea after the second postpubertal estrus

Item	No. of gilts	No. of corpora lutea	Slaughter wt, kg
Line[a]			
CO	106	13.5 ± 0.27**	120.8**
OR	121	16.2 ± 0.26	113.9
Season			
Spring-born	107	14.3 ± 0.27	111.6**
Fall-born	120	15.4 ± 0.26**	121.3

[a]CO = control line and OR = line selected for ovulation rate.
**$P < 0.01$ for comparison between lines or seasons.

as early as 34 d of age (Ford et al., 2001). In all gilts of the current study, plasma FSH concentrations at 65 d were correlated significantly with FSH concentrations at 75 and 85 d ($r = 0.52$ and 0.33, respectively), confirming that a subpopulation of gilts experienced greater exposure to endogenous FSH than other gilts. Yet ovarian weight at 85 d was not associated with FSH at 65 d. Also, this lack of a relationship between FSH and ovarian weight remained when the population of gilts was restricted to only those that had antral follicles at 85 d. Moreover, some of the gilts with the greatest FSH concentrations at 65 d had small ovaries, lacking visible antral follicles on d 85. These observations indicate that some component of ovarian development in addition to the duration of exposure to FSH compromises the response of ovarian follicles to endogenous FSH.

The age at first detected estrus did not differ among gilts of the CO and OR lines and confirms the findings of Wise et al. (1980) that selection for a greater number of ovulations does not impact pubertal development in gilts. However, with the selection procedures used by Ruiz-Flores and Johnson (2001), selection for ovulation rate and number of fully formed pigs at birth decreased the age at puberty. Fall-born gilts were older at first estrus than spring-born gilts. This differs from the small, unfavorable effect of decreasing day length (birth in the spring) on pubertal development of gilts reported by others (Christenson, 1981; Paterson and Pearce, 1990; Tummaruk et al., 2000) and from the absence of a seasonal effect reported by Signoret et al. (1990). The proportion of gilts detected in estrus by 250 d of age was 90% or greater in OR gilts and in fall-born CO gilts, but, in spring-born CO gilts, only 78% achieved puberty. This observation implies that a subpopulation of the spring-born CO gilts may be predisposed to some adverse effect of their environment whereas the remainder of the CO gilts and all of the OR gilts experienced pubertal development more rapidly than all of the fall-born gilts. This poorer reproductive development of spring-born CO gilts cannot be attributed to poorer growth rate because CO gilts grew at a faster rate than spring-born OR gilts. No explanation exists for the effect of season on growth rate; however, Tummaruk et al. (2000) observed a similar seasonal effect on the growth rate of gilts. After adjustment for effects of sea-

son, the age at first detected estrus was not correlated with BW at 154 d of age. We conclude that selection for a greater number of corpora lutea in gilts had a minor effect on pubertal development, leading to the conclusion that increased FSH secretion in prepubertal OR gilts relates more to the synthesis and secretion of FSH than to a difference in the stage of pubertal development in these two lines. The observation that ovarian weight at 85 d of age was not related to age at first estrus provides additional support for the concept that differences in puberty in females reflect differences in the rate of hypothalamic development.

Gilts used in the current study represent genetic lines available in the 1970s that were characterized by slower growth rate and greater fat deposition than lines of pigs currently used in pork production (Cassady et al., 2002a, 2002b). In gilts of these fatter, slower growing lines, moderate restriction of feed intake during prepubertal development generally produced no effect or had a stimulatory effect on age at puberty (Aherne and Kirkwood, 1985). To date, attempts to establish that puberty in leaner, faster growing lines of gilts requires a critical BW, a critical amount of fat deposition, and so on have proved inconclusive (Rozeboom et al., 1995; Klindt et al., 2001; Patterson et al., 2002). Rather, there is a complex interaction including genotype, the age when feed intake becomes restricted, the age when daily evaluation of estrus begins, and a series of other environmental factors (Hughes et al., 1990). In the current study, in which sire and litter were adjusted in the statistical analysis, BW at none of the ages from birth to 154 d was associated with the age at puberty, but BW at weaning and subsequent ages was associated with ovulation rate. The CO gilts grew more rapidly than OR gilts; fall-born gilts grew more rapidly than spring-born gilts, but these differences in growth rate were not associated with differences in ovarian weight at 85 d. The objective was to compare d-85 ovarian weight and the age at first estrus in these two lines of gilts using a feeding regime similar to that employed during their 10 yr of selection.

The induction of puberty in gilts with boars having fence-line contact is less effective than direct physical contact (Hughes et al., 1990). However, Zimmerman et al. (2000) reported that the age at first detected estrus

differed in gilts from two genetic lines that varied in their rates of sexual development whether they received fence-line contact or direct contact with boars. The mean age at puberty was greater with fence-line contact than with direct boar exposure. Furthermore, direct physical contact was more effective when provided to gilts at 130 d than at 154 d of age (Zimmerman et al., 2000). The age at puberty in the current study was intermediate between the 198 d reported by Cassady et al. (2002b) in the foundation genetic line of these gilts and the 217 d in gilts of this same four-breed composite that were maintained in a different far-rowing season (Christenson et al., 1993). Both of these studies used direct physical contact with boars for daily detection of estrus (K. A. Leymaster and R. K. Christenson, personal communication). Collectively, the two lines of gilts evaluated in the present study had similar rates of pubertal development under the environmental conditions used. Lines were commingled in pens, and the personnel collecting the estrous data were unaware of the genetic line of each gilt.

Implications

Direct selection for a greater number of corpora lutea produced greater plasma concentrations of follicle-stimulating hormone during pubertal development, but this response to selection had no apparent influence on the rate of ovarian development. Therefore, greater concentrations of endogenous follicle-stimulating hormone indicate a greater capacity to synthesize and secrete follicle-stimulating hormone rather than an alteration in the rate of sexual development.

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